Paleobotanical Evidence of Mesozoic and Cenozoic Climatic Changes

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INTRODUCTION

Since the geologic record does not contain any direct evidence of climate *per se,* paleoclimatic studies must rely entirely on indirect evidence. As a result, only inferences and interpretations variously based upon studies of either the fossil record or the sedimentary record can be made. From the paleontological record, fossil land plants have generally been accepted as the most reliable "thermometers of the ages." Such confidence is based upon the recognition that the distribution of modern land plants is primarily controlled by climatic conditions. The distribution of terrestrial vertebrates, on the other hand, tends to follow food supply rather than climatic zonation. Many animals, moreover, can escape the rigors of unfavorable seasons by burrowing, hibernating, or migrating, whereas all woody plants must remain rooted in situ and tolerate the unfavorable season along with the favorable.

The nature of the fossil plant record and its relationship to modern plants has predetermined the three contrasting methods which have been applied to studies of ancient climates:

1). Quaternary methods are based almost entirely on microfossils—pollen and spores—referable to modern taxa whose climatic requirements are reasonably well known.

2). Methods concerning Tertiary and Late Cretaceous plants are based largely on megafossils, chiefly the leaves of dicotyledons; among living groups these are the most definitive and reliable climatic indicators. Relationships to modern taxa, however, become less and less certain with increasing age of the floras involved.

3). Inferences concerning Early Cretaceous, Jurassic, and Triassic climates depend upon fossil cycads, conifers, ginkgos, and ferns which become more and more distantly related with increasing age to living genera, or even to living families. The more useful dicotyledons are rare in Lower Cretaceous deposits and are not reliably recorded from either the Jurassic or the Triassic.

BASIC PREMISES

Inferences concerning ancient climates based on studies of fossil floras depend primarily on the uniformitarian principle of the present as the key to the past. It is assumed, unless there is good evidence to the contrary, that plant taxa of the past lived under the same climatic conditions as they

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or their nearest relatives do at the present time. Some doubts, however, have been cast as to the infallibility of these basic tenets:

In the first place, the present climatic conditions are apparently abnormally cold in terms of the inferred climates of the earth during the past one hundred million years or so. Moreover, the rapid climatic fluctuations of the recent past, from glacial to nonglacial conditions, also appear to have been abnormal and to have resulted in major plant migrations from which the earth's vegetation may not yet have had time to fully recover. There is apt to be a lag in the readjustment of plants to their preglacial environments, especially within regions covered by fresh glacial deposits.

In the second place, it has occasionally been argued that there is a possibility that plants may have changed their climatic requirements during Tertiary time. It is true, for example, that a few normally tropical or subtropical families have indeed produced species whose acquired climatic tolerances permit them to thrive under temperate conditions, as for example, magnolias and persimmons in northeastern United States. Also, from normally temperate woody ancestors, the arctic willow and the dwarf birch have developed tolerances enabling them to survive under the frigid conditions of the tundra. Such anomalous forms are few in number, however. A recent suggestion that many, if not most, plant taxa have undergone changes in climatic tolerances during Tertiary time (Wolfe, 1969, p. 34) does not seem to be borne out by present-day distributions. To overcome the misleading paleoclimatic inferences suggested by a few anomalous forms in a fossil flora, it has become the general practice to rely on the evidence of the total assemblage rather than on a few individual species. To suggest that the 25 or more species of a plant community should all change their climatic tolerances is taking unwarranted liberties with the laws of chance.

A second basic premise is the belief that plant communities are able to migrate more readily than to adapt to changing environmental conditions, including climatic. Vertical sequences of fossil floras have shown successive replacements of the older plant communities by communities of quite different composition. Regional studies have indicated that the majority of the plants were shifted to new areas, with or without the development of new species. Lesser numbers of the plants were unable to shift along with the changing environment and so became extinct. Even fewer of the plants were able to adapt, usually by speciation, to the changing environment and remain at or near their original habitats.

An example of the changing character and migrations of major plant communities in western North America during Tertiary time is shown in Fig. 1.

Another basic premise is the general conviction that a reasonably large collection of plant fossils from a particular deposit accurately represents the vegetation which at one time grew in the vicinity of the depositional basin. Although this may be true qualitatively, there are a number of fac-

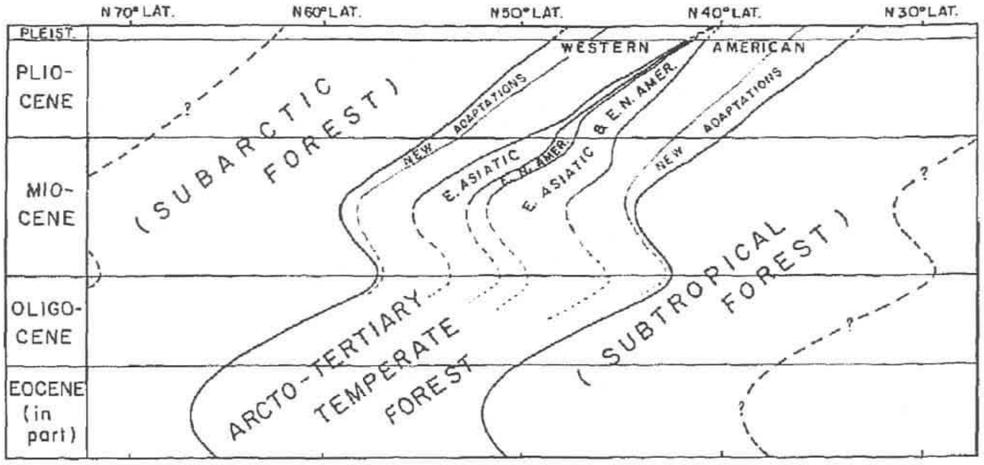

FIG. 1. Generalized sketch showing movements of the Arcto-Tertiary temperate forest of western North America in both space and time, involving: 1). migrations; 2). adaptations; and 3). exterminations. (Dorf, 1964)

tors which must be considered before such a fossil collection can be evaluated in quantitative terms. Chaney (1959, p. 22–26) has recently discussed the various factors affecting the actual numerical representation of plant megafossils, in part as follows:

"1). Depositional factors: These are the most significant for our discussion, affecting as they do the opportunities for leaves and fruits to enter the fossil record. The five factors now recognized are listed in approximate order of importance: a). proximity of the parent plants to the site of deposition; b). durability of the organ entering the record; c). weight-area of the organ entering the record; d). height and volume of the parent plants; e). deciduous versus evergreen habit of the parent plants.

"2). Recognition factors: Some leaves and fruits are of so generalized aspect that they are not readily recognized, and tend either to be ignored or to be incorrectly placed taxonomically.

"3). Correction factor for compound organization: This must be applied to the count of leaves and other organs which are regularly divided and separated prior to deposition, so that the units found in the fossil flora do not represent a complete foliar organ."

As applied to the microfossil plant record, palynologists have recently also become aware of the lack of quantitative correspondence between the pollen record and the proportional representation of plants in the adjacent living community. This is discussed below under "Quaternary Developments: 4)."

QUATERNARY CLIMATES

The Plant Record.

It is a well known fact that the time-stratigraphic divisions of the Quaternary are based primarily upon paleoclimatic inferences (Amer. Comm.

Strat. Nom., 1961, art. 39). These inferences have been made mainly on the basis of the plant microfossil record, which is almost exclusively composed of well preserved pollen and spores. The megafossil record is only fair to poor and is only recently being used to supplement the microfossil record.

The Quaternary plant record is a short one compared to that of any other geologic period. The span of time involved has been variously estimated at not less than 300,000 years nor more than 2,000,000 years. As a consequence—and in contrast to the record of land mammals—there was apparently no appreciable amount of evolution among the great majority of woody land plants; nearly all pollen grains and spores are morphologically similar to those of living taxa. This has materially enhanced their value as paleoecological (including paleoclimatological) indicators.

Unfortunately, although most pollen grains and spores can be identified to the generic level, very few are readily determinable to the specific level. This obviously detracts from the usefulness of many forms for paleoclimatic purposes; living pines (*Pinus*), for example, include many different species which range climatically from subtropical lowlands to both subarctic lowlands and frigid, alpine uplands; among dicotyledons, willows (*Salix*) and birches (*Betula*) also include some species acclimated to temperate lowlands and others equally at home in the cold tundra of the north.

The writer does not intend to discuss further the Quaternary plant record as related to paleoclimates, as this field is quite removed from his own research endeavors. Further information and references on the use of pollen and spores in geology may be found in Leopold and Scott (1958).

Quaternary Developments.

Of many recent developments the following seem to the writer to be of general interest as related to paleoclimatic studies:

1). Though still in its early stages, the invention and application of the scanning microscope to the field of palynology should add greatly to the use and knowledge of Quaternary pollen and spores. It should hopefully make it possible to see characters previously not detectable which would permit identifications of most forms to the specific level. This would materially enhance their value as paleoclimatic indicators.

2). The evidence is steadily becoming more convincing that the north–south displacements of vegetation zones, as the result of recurrent glacial and interglacial climatic changes, were of major proportions. Although first suggested nearly a hundred years ago, this interpretation of the plant record has not been generally accepted by most paleobotanist and botanists. In the last fifteen years, however, an increasing amount of impressive evidence has come to light. This includes the finding of numerous Canadian boreal plants in the Pleistocene deposits of the Gulf coast and southeast Atlantic coast lowlands, as well as the replacement in the southwestern states of lowland desert vegetation by upland forests as the inferred result of glacial climatic conditions (Deevey, 1965; Martin and Mehringer, 1965; Whitehead, 1965).

3). There is a growing contention that the pollen records south of the Pleistocene terminal moraines do not show any earlier glaciations comparable in severity to the Wisconsin glacial maximum (Deevey, 1965). It seems clear that several more long Pleistocene cores will have to be studied in greater detail in order to substantiate so startling a bit of negative evidence.

4). Much recent work has been done by palynologists on the study of modern pollen rain as fallout in bottom deposits of lakes and ponds, to determine the relation of the buried pollen record to the surrounding vegetation (Davis, 1963; 1965). From these studies it has been concluded that the pollen record from a particular locality is usually not an accurate representation of the adjacent nearby community, not even qualitatively. This condition is apparently in large part due to four factors: a). contamination by pollen grains transported from remote regions to the depositional site by either wind or water; b). over-representation of certain forms due either to nearness of the parent plant to the depositional site or the unusually prolific amounts of pollen shed by certain nearby plants, such as pines (*Pinus*) and hazels (*Corylus*); c). under-representation of certain forms which do not produce much pollen, such as maples (*Acer*), or whose pollen is easily destroyed in the selective processes of fossilization, such as linden (*Tilia*); d). contamination by pollen grains derived by erosion and redeposition from older deposits nearby. All of these factors must be considered and evaluated in terms of any paleoecological inferences, including paleoclimatic, based on the pollen record.

5). It has become increasingly clear that not enough is yet known about the ecological requirements and tolerances of many living species of plants to be truly definitive in paleoecological studies, including paleoclimatic interpretations. Investigations are needed in determining the relative importance as limiting factors of not only climate but also soils, topography, competition, and normal succession. The construction of more accurate range maps of modern plant distributions are also highly desirable.

6). In both the midwestern and southwestern regions of the United States there is new evidence suggesting an unusually rapid, rather than the presumed gradual, recovery of postglacial vegetation following the Wisconsin glacial maximum. Ogden, for example, interprets the replacement of spruce forest by more southerly forests to have taken place in about 170 years in Minnesota and in about 1160 years in Ohio. This replacement is equivalent to a 600 mile migration on the surface. The cause of so rapid a recovery is believed to have been a "rapid and dramatic change in temperature and/or precipitation" (Ogden, 1967). Corroborative evidence from other localities will obviously be sought.

7). The steadily growing volume of Pleistocene and post-Pleistocene

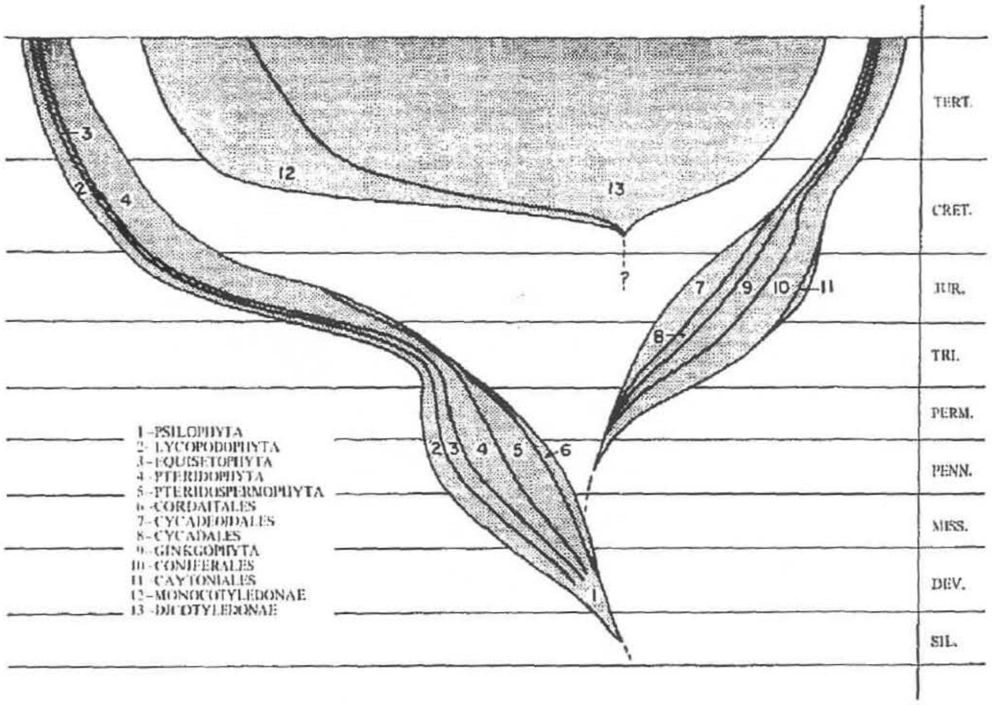

FIG. 2. Geologic distribution of the components of the three major terrestrial floras. (Dorf, 1955)

palynological research has clearly strengthened the belief that there were no major extinctions among North American plants in the Late Pleistocene. This was the time when a number of major American extinctions took place among the land mammals—horses, camels, elephants, ground sloths, etc. To account for such wholesale extinctions among the mammals, it is apparent that causes must be sought that did not affect plant life in any appreciable way. In the Pleistocene of Europe the extermination of a number of plant species is generally attributed to east-west mountain chains, which were barriers to the north-south shiftings of vegetation zones. There is growing evidence that the mammalian extinctions were caused, or at least accelerated, by ancient Man (Martin and Wright, 1967).

LATE CRETACEOUS AND TERTIARY CLIMATES

The Plant Record.

In contrast to the emphasis on microfossils in the record of the Quaternary Period, work on floras of Late Cretaceous and Tertiary age has been primarily on megafossils, chiefly the compressions of leaves. These appear to belong almost exclusively to the angiosperms, of which the dicotyledonous remains overwhelmingly outnumber the remains of monocotyledons, as shown in Fig. 2. Much less common, though of considerable importance, are the remains of seeds, fruits, and wood of angiosperms, as well as fern foliage, conifer twigs, needles, cones, and seeds. Very rarely are there occurrences of the remains of angiosperm flowers or of fruiting structures of lower plant groups. Unfortunately, the plant record is essentially one of woody plants; the nonwoody herbs are very poorly represented, except in the pollen record.

Although the Tertiary microfossil record of both pollen and spores is an excellent one, its application to paleoecology has been neglected by all but a few palynologists. In contrast to the interests and efforts of Quaternary palynologists, Tertiary palynologists have tended to focus their attention on the widespread use and reliability of pollen grains and spores in subsurface correlations.

Collections.

An important preliminary to the use of Late Cretaceous and Tertiary floras as paleoclimatic indices is the recovery of an adequate sample. Climatic inferences should rarely be based on fewer than 25 species. For statistical analyses of the morphological features of the plant remains, discussed below, a total of at least 500 specimens should be collected if at all possible; 1000 specimens would be preferable.

The technique of finding, collecting, and preparing an adequate sample of megascopic terrestrial plant remains has been fully discussed elsewhere (Dorf, 1965).

Use of morphological characters.

During the past few decades it has become increasingly clear that certain morphological features of the leaves of woody dicotyledons (dicots) may be used as climatic indicators, wholly independent of the taxa to which the leaves belong. As far back as 1915 I. W. Bailey and E. W. Sinnott investigated dicot leaves from the tropics to the tundra. Their investigations indicated that there is a clear cut correlation between easily observable characters of the leaves and the climatic conditions under which they grew (Bailey and Sinnott, 1916). They were also the first to recognize the importance of these observations to the study of geologic climates on the basis of fossil leaf characters independent of taxonomic affinities (Bailey and Sinnott, 1915). The application of these observations to Late Cretaceous and Tertiary floras by various workers has added greatly to the reliability of their paleoclimatic interpretations (Chaney and Sanborn, 1933; Dorf, 1938; MacGinitie, 1941; Wolfe, 1969).

In the writer's opinion, certain leaf characters have greater value than others for paleoclimatic investigations, namely marginal features, length, and venation. These three characters are regarded as more reliable than other leaf characters mainly because they have been more fully investigated and tested in modern vegetation. For example, leaves of large size (over 10 cm.) with entire margins and pinnate venation have been found to occur most abundantly in the lowland tropics and to decrease proportionately in the cooler temperate lowlands or tropical uplands. These same three features are also more objectively observable in fossil leaves than are the remaining characters of texture, organization (simple or compound leaves) and presence or absence of an elongate drip-point. Each of these leaf characters and its relevance to paleoclimatic studies will be presented below:

1). The most reliable leaf character for paleoclimatic studies, in the writer's opinion, is the nature of the leaf margins of woody dicots, namely, whether they are entire (smooth, without teeth) or non-entire (variously toothed, indented, or lobed). These features show major differences in comparing forest vegetation ranging from the tropical lowlands to the lowland subarctic, as well as to the cool and frigid uplands. Entire margins are characteristic of the leaves of over 75% of the woody dicot species in moist, lowland tropical forests. Examples of average percentages of entire leaved species living under different climatic conditions are as follows (Bailey and Sinnott, 1915; 1916):

	Percentages of entire-margined leaves	
Cold Temperate	*Trees*	*Shrubs*
East-central North America	10	37
Rocky Mountains	0	40
Central Russia	0	36
England	3	37
Warm Temperate		
Southeastern United States	36	54
Los Angeles	18	58
Spain	13	59
East-Central China	38	52
Subtropical and Tropical		
Florida Keys	84	83
West Indies	88	71
Hong Kong	73	71
Brazil	90	87

In the tropics of Hawaii and Ceylon it is significant to note that in the cooler uplands there is an appreciable decrease in the proportion of entire-margined leaves, as follows (Bailey and Sinnott, 1916, p. 28):

	Percentages of entire-margined leaves	
	Trees	*Shrubs*
Lowlands, Hawaii	84	71
Uplands, Hawaii	71	50
Lowlands, Ceylon	85	81
Uplands, Ceylon	72	75

In the cold temperate forests of eastern North America the few entire-leaved dicots which do live there (± 10%) are mostly forms which are not common and whose occurrences within these forests are close to the northern limit of their optimum development under more southerly warmer conditions. Typical of such species are: *Quercus phellos* L.; *Quercus imbricaria* Michx.; *Cercis canadensis* L.; *Nyssa sylvatica* Marsh.; *Magnolia virginianum* L.; *Diospyros virginiana* L.

Even at the family level, there are many groups of woody, entire-leaved dicots which are virtually absent from any of the northern, cold temperate forests. Examples include such well known families as the Lauraceae, Rhizophoraceae, Ebenaceae, Anonaceae, and Sapotaceae (Bailey and Sinnott, 1916).

There do exist a few environmental situations where entire-leaved dicots are dominant, yet the climate is not warm. These are the very cold arctic and high mountain habitats, or other physiologically dry areas, such as deserts and salt flats. A fossil assemblage of this type could readily be recognized, however, by the very small size of the majority of the dicot leaves.

Non-entire dicot leaves include those which possess teeth of any sort and size, indentations, or lobes. Such leaf types increase from roughly 20% in the moist lowland tropics to 80% or more in the moist cold temperate forests of higher latitudes and mountain uplands. Bailey and Sinnott (1915, p. 833), for example, found that in the cold temperate, mesophytic forests of eastern North America (east of the Great Plains and between latitudes 40° and 50° North) 86% of the dicot shrubs and 90% of the dicot trees had leaves which were non-entire, being variously toothed or lobed. They also observed (Bailey and Sinnott, 1916, p. 30) that in the forests of the moist tropical lowlands, the relatively few dicots with toothed or lobed leaves (less than 30%) are usually small trees or shrubs, or climbing plants, living chiefly in protected, comparatively cool habitats. Most of these moreover, possess vestigial or only rudimentary teeth showing signs of reduction.

2). In general usage, comparatively large leaves, i.e., megaphylls, are those whose average length is 10 cm. or over. The dominance of such large leaves in a modern flora is indicative of lowland, tropical forests in regions of adequate rainfall throughout the year (Bailey and Sinnott, 1915, p. 833). In the tropical forest of Panama, for example, 56% of the woody dicots possess large leaves. In the temperate forest of the central Coast Ranges of California only 27% of the woody dicots have large leaves (Chaney and Sanborn, 1933, p. 20).

Relatively small leaves, i.e., microphylls, average less than 10 cm. in length. These are the dominants (60% to 90%) in temperate forests, increasing proportionately poleward in latitude and upward in altitude.

Leaf size categories generally also include a consideration of leaf blade area. Megaphylls generally are 2700 sq. mm. or over in area, microphylls less than 2700 sq. mm. (Leaf blade area = approximately length × maximum width × ⅔).

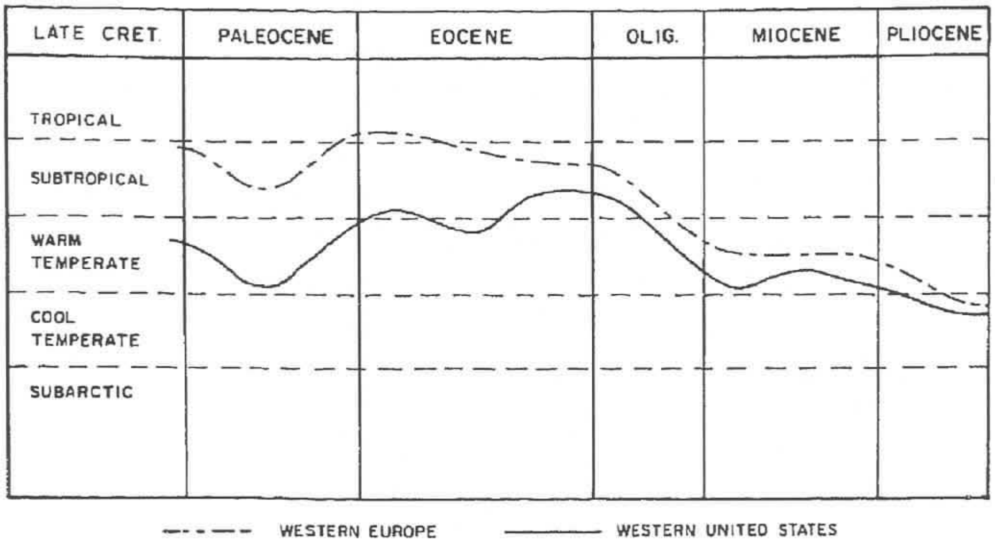

FIG. 3. Curves illustrating the inferred climatic regimes of western Europe and western United States. (Dorf, 1964)

3). Venation refers to the pattern of the veins on a leaf blade. In woody dicots the venation is normally either pinnate (a single primary midvein with bilaterally arranged secondary veins) or palmate (three or more radiating primary veins with bilaterally arranged secondary veins). Pinnate venation is considerably more common in tropical (± 85%) than in temperate forests (± 75%). Palmate venation combined with palmate lobes, as in maples (*Acer*) and sycamores (*Platanus*), is very rare—less than 2%—in the tropics, but fairly common (5 to 10%) in temperate environments (Sinnott and Bailey, 1915, p. 2, 3). Palmate venation in short, more or less heart shaped leaves, usually with extended tips, is typical of climbing lianas which are fairly common in tropical rain forests and very rare (2% or less) in temperate forests (Wolfe, 1969).

Recent observations on modern leaves have shown that the density of the venation and the characteristics of the finer tertiary venation can also be correlated with climatic differences. Wolfe (1969, p. 35) has pointed out that in tropical dicot leaves there is a "pronounced tendency for the lamina to be supplied with many veins," resulting in a closed network of very small areoles; in the leaves of temperate dicots, on the other hand, there are generally fewer veins and an open network of highly branching, freely ending tertiary veinlets.

In the application of venation characteristics of fossil dicot leaves to paleoclimatic studies, it is unfortunate that there are many instances where the preservation is such that the details of the finer tertiary venation cannot be seen.

4). Another leaf character with climatic implications is the presence or absence in a dicot leaf of an elongated, drawnout apex or tip, generally known as a drip point, dripping point, or drip tip. Drip points are especially common on dicot leaves in moist, tropical lowland floras. Chaney has reported the presence of drip points on the leaves of 76% of the dicot species in the tropical lowland forest of Panama, contrasted with only 9% in the lowland temperate forest of west-central California (Chaney and Sanborn, 1933, p. 19).

The drip point character is sometimes difficult to apply to fossil leaves, as an attenuated leaf tip, by its very nature, is often quite fragile and easily broken off during the processes of fossilization. This situation can usually be remedied by collecting a large enough suite of specimens of each species to insure at least one which has the full apex preserved.

5). Dicot leaf textures are generally referred to as either thick or thin. Thick textures are typical of the large leaves in tropical plants, whereas thin textures are more common among temperate forms. Strangely enough, thick textures are also to be found in the dicot leaves of frigid and arid environments, or other physiologically dry regions. In such situations, however, the leaves are nearly always quite small.

In their work on the Goshen flora of Oregon, Chaney and Sanborn (1933, p. 19) found that 98% of the dicot leaf remains appeared to be of thick texture, comparable to the percentage observed in the living tropical forest of Panama. In contrast, the temperate forest of west-central California showed only 64% thick textured leaves.

Textural qualities of fossil leaves cannot always be applied to paleoclimatic studies because inadequate preservation may make it difficult to determine the texture of the original leaf.

6). In organization, dicot leaves are either simple or compound, that is, made up of leaflets attached to a common, long petiole. Although this character has often been suggested as of relevance to paleoclimatic studies, its reliability seems rather doubtful for two reasons: in the first place, it is difficult to determine whether fossil dicot leaves are simple or compound except by a positive taxonomic reference to living taxa. Such a requirement defeats the original purpose of using this character independently of systematic relationships. Secondly, there is apparently not sufficient consistency in the modern occurrence of compound leaves. Webb (1959, p. 555), for example, in his study of Australian rain forests, found the following percentages of compound leaves:

	Per cent
Cool temperate	0
Warm temperate	10–30
Subtropical	30–40
Tropical	15–50

In the tropical forest the downward range from 50% to 15%, a figure comparable to that observed by Chaney in the tropical forest of Panama

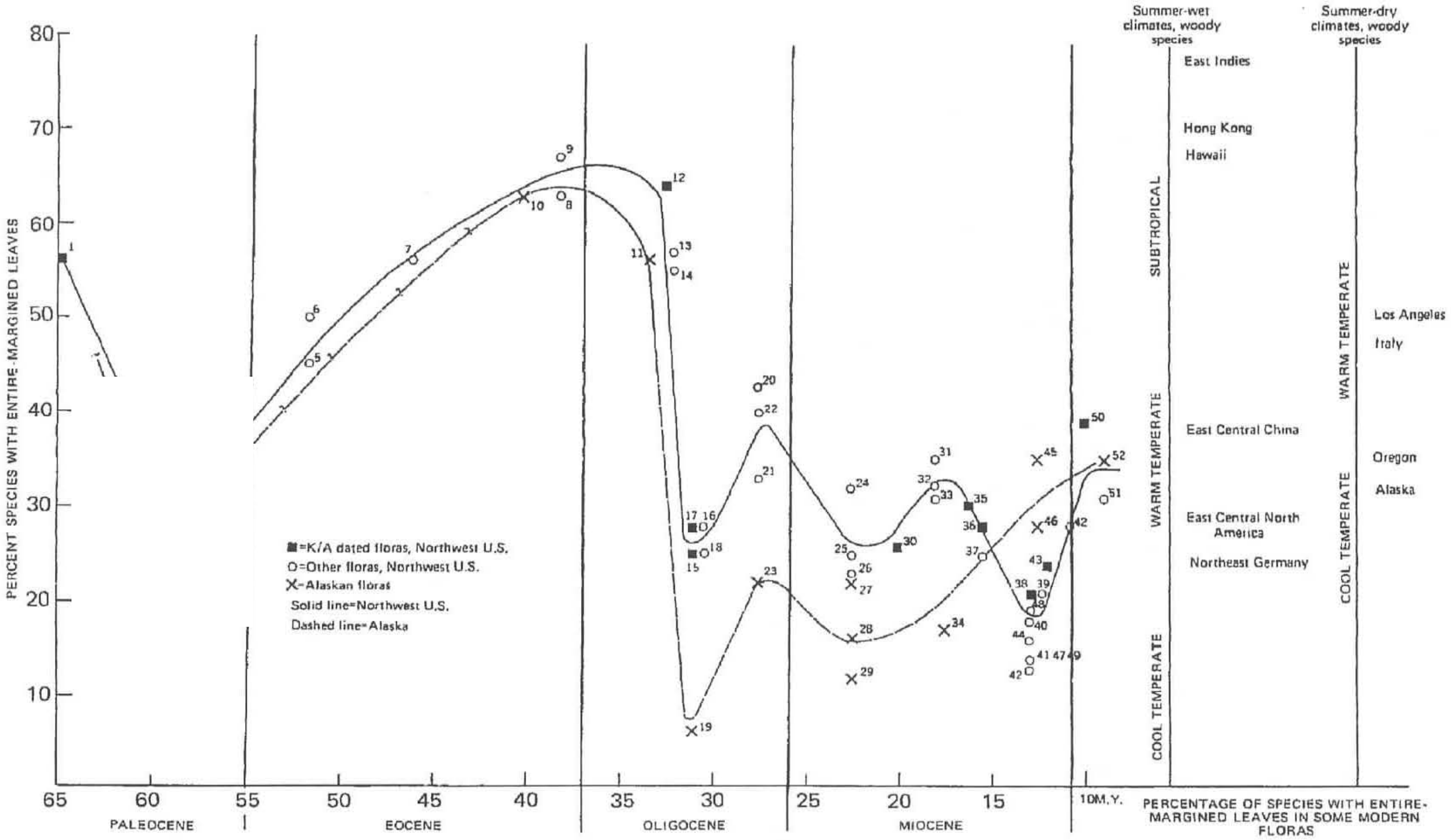

FIG. 4. Leaf margin curves based on Tertiary floras of northwestern United States and Alaska. (Wolfe and Hopkins, 1967)

(Chaney and Sanborn, 1933, p. 19), is too great to be of value in relation to climatic correlations. Moreover, the complete absence of compound leaves in the cool temperate Australian forests does not correspond to their fairly common occurrences in the corresponding zones of the northern hemisphere.

Systematics.

In paleoclimatic investigations of Late Cretaceous and Tertiary plants, morphological studies should be followed by the accurate identification of the taxa present in the fossil flora. Identification of dicot leaves, which are usually the most abundant plant remains, depends upon careful consideration of as many of the following characters as are well preserved: 1). shape and dimensions of the leaf blade, including ratio of length to width, relative position of greatest width, and range of variability; 2). shape and character of the apex and base of the leaf; 3). marginal characters—entire or non-entire—and, if present, the kind, number, and disposition of the marginal teeth or lobes; 4). venation pattern, that is, whether pinnate or palmate, together with the number, character, and arrangement of the primary, secondary, and tertiary veins; 5). texture (thick or thin); 6). petiole characteristics such as relative length and method of attachment to the leaf blade; 7). microscopic details of the leaf cuticle, including sizes, shapes, and arrangements of stomata, if preserved. In all details, comparisons should always be made with the leaves of modern taxa, readily available at botanical gardens and herbaria.

Other identifiable plant remains, often found associated with the leaves, are seeds and fruits, conifer foliage and cones, petrified wood, and very rarely flowers or flower parts. For accurate identifications, these should be morphologically compared, both megascopically and microscopically, with both modern and fossil plant materials. If available, the pollen and spore assemblage should also be studied and compared taxonomically with the generic and specific identifications of the megafossils.

In younger Tertiary floras many of the plant remains have been found to be indistinguishable from comparable portions of modern species. These species are often found living in regions not far distant from the fossil locality. Progressively older Tertiary floras contain fewer and fewer plant remains referable to living species; these forms, however, usually show definite relationships to modern genera. Most of these are found living today in regions progressively farther and farther removed from the fossil locality as the floras increase in age. In Late Cretaceous floras, and to some extent in Paleocene and Eocene floras, the plant remains can usually be allocated to modern families, but are rarely referable to living genera. In these older floras it has often been found that modern relationships are with taxa whose present day distribution is very distantly removed from the fossil locality, indeed often on a different continent or hemisphere. Finally, in

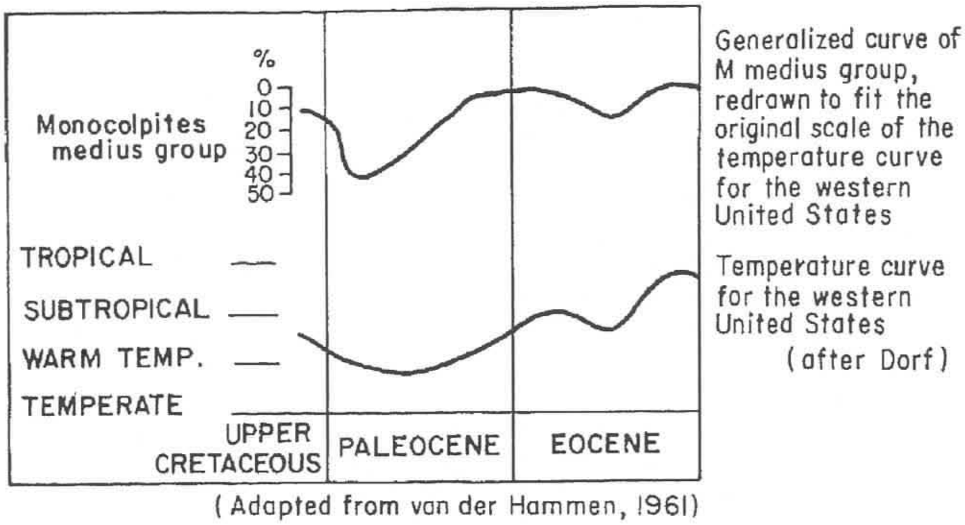

FIG. 5. Temperature curve for the western United States, based on plant macrofossils, compared with a curve based on a pollen diagram from Colombia.

progressively older Cretaceous floras many of the plant remains are not referable to any known living taxa.

From these taxonomic observations it has obviously been concluded that the older the flora the less reliable are its paleoclimatic implications. Taxonomic and stratigraphic studies of successive floras have led to the conclusion that major changes in the earth's vegetation took place during the time from the Late Cretaceous to the end of the Pliocene. These involved evolutionary as well as distributional changes, both of which apparently proceeded very slowly during the span of over 120 million years. This is a very different history from the rapid, mainly distributional, changes which occurred during the very short Quaternary Epoch. In the pre-Quaternary and the Quaternary, however, both the floristic and the vegetational changes are generally believed to have been due to major changes in environment, of which climate is regarded as of primary importance. Other secondary controls, both physical and biologic, have been considerably more difficult to infer on the basis of fossil floras.

Tertiary Developments.

Among the more interesting developments in the study of Tertiary climates have been the new and conflicting interpretations concerning the climatic changes from the Paleocene through the Pliocene Epochs. There is general agreement that there was a world wide change from warmer to colder climates from the early to the late Tertiary, with a period of maximum warmth in the Late Eocene or Early Oligocene. There is also a general consensus that the fluctuating changes from glacial to nonglacial climates during the Pleistocene, as inferred from the physical record, are supported by evidence

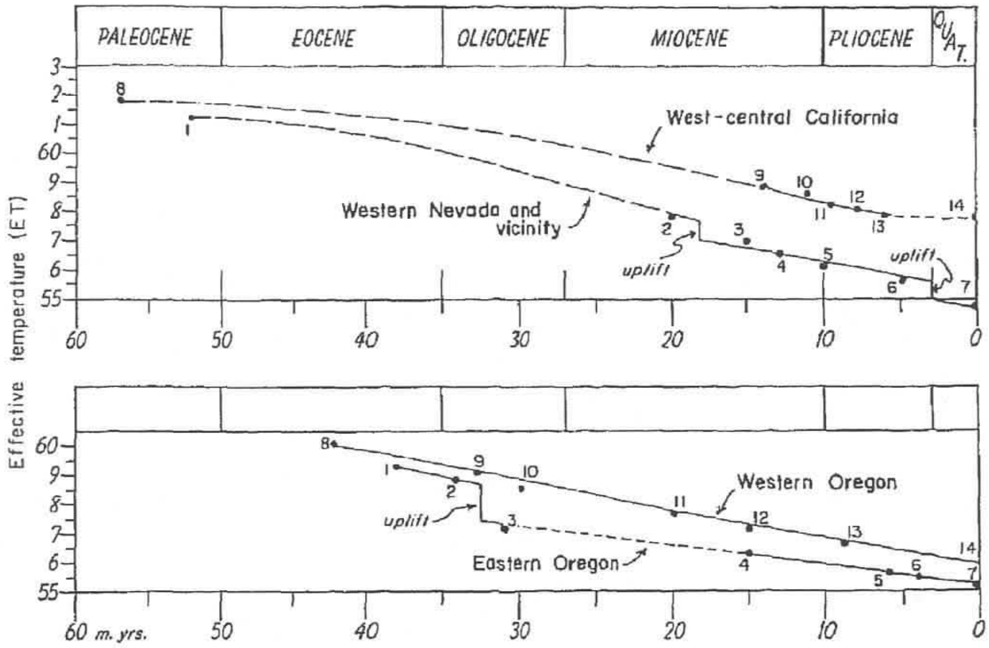

FIG. 6. General cooling trend shown by tertiary floras in Western United States, as judged from effective temperature (Axelrod and Bailey, 1969).

from the plant record. There is disagreement, however, as to whether the cooling trend between the Early Oligocene and the beginning of the Pleistocene was a steady, gradual trend or was marked instead by a few to perhaps many major fluctuations.

A generalized curve showing alternating warmer and cooler climates during the Tertiary of western United States was first attempted by the writer about fifteen years ago (Dorf, 1955, Fig. 3). This fluctuating curve was slightly modified a few years later on the basis of new information on the age relationships of certain western Tertiary floras (Dorf, 1964, Fig. 2). As reproduced here in Fig. 3, this curve shows warmer episodes in the latest Cretaceous, Early Eocene, Late Eocene-Early Oligocene and mid Miocene, alternating with cooler episodes. The figure also includes the writer's interpretation of the fluctuating climatic regime in western Europe during the Tertiary. The correspondence between the two curves is fairly close, assuming that the available data was correctly interpreted.

Since that time several Tertiary climatic curves have been presented by other writers, on the basis of either new collections, new data from other regions, or different interpretations of the same data. New and largely unpublished data obtained by Wolfe and Hopkins led to the construction of a Tertiary climatic curve for northwestern United States, shown here in Fig. 4, which differed from the writer's in several respects: 1). absence of a temperature high in the Early Eocene; 2). an additional temperature-high in the Late Oligocene; and 3). another temperature-high in the Pliocene

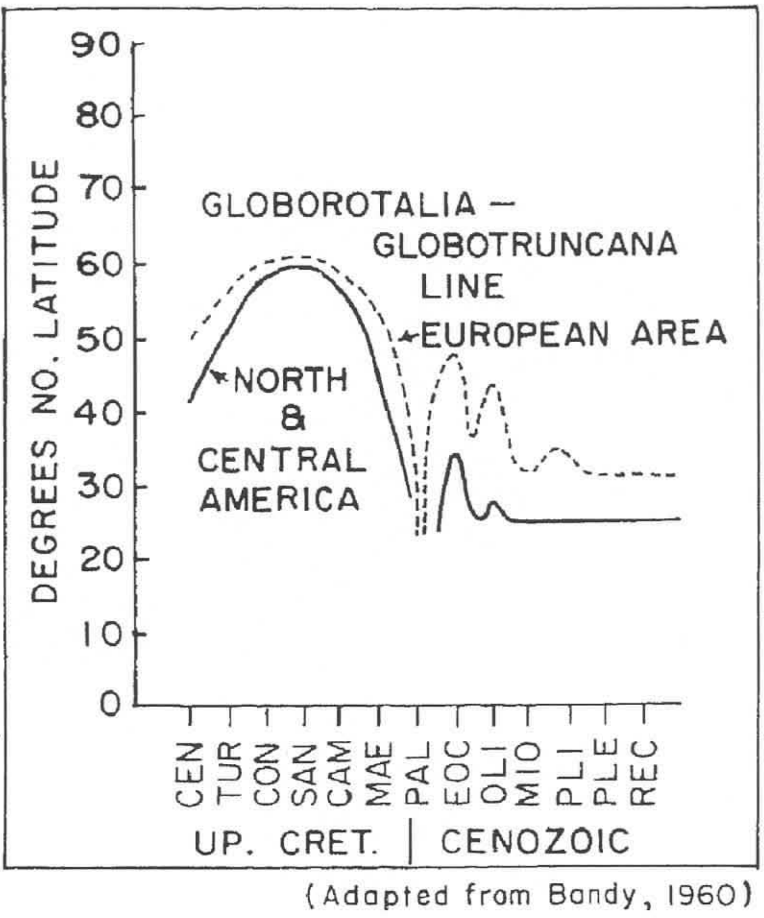

FIG. 7. Paleoclimatic trends based on planktonic foraminiferal criteria.

(Wolfe and Hopkins, 1967, Fig. 3). The Oligocene and Miocene portions of their climatic curve are based on especially good control; the control points for the Paleocene and Eocene are more widely spaced. More recently, Wolfe (1969, p. 67) has postulated warmer episodes in both Early and Late Eocene, separated by a cooler phase in the Middle Eocene. These are essentially the same trends as shown in the writer's 1964 climatic curve of the Eocene.

Pollen analyses from northern South America enabled van der Hammen (1961) to present a climatic curve for the Paleocene and Eocene, shown here in Fig. 5, with essentially the same fluctuations as in the writer's interpretations. Van der Hammen also suggested a hypothesis, in part based on his pollen evidence, that Tertiary time was marked by numerous climatic maxima and minima, with 4 in the Paleocene, 9 in the Eocene, and 9 in the Oligocene. He proposed that each pair of high temperature peaks was roughly two million years apart. In complete opposition to this extreme view is the more conservative one, supporting a gradual, steady climatic change, illustrated

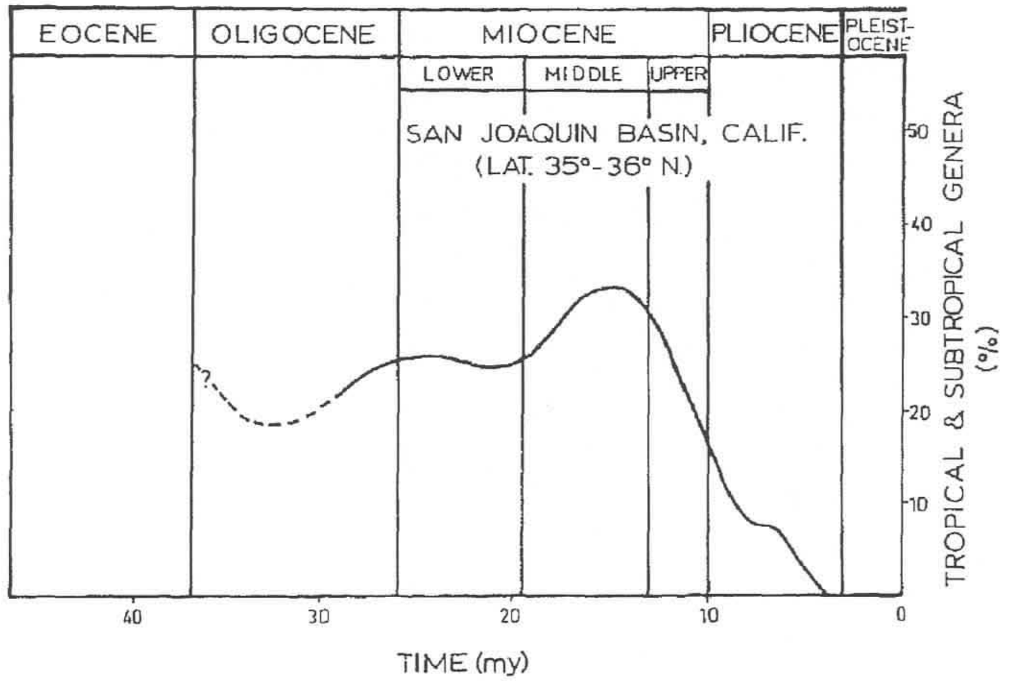

FIG. 8. Tertiary paleoclimatic trends in the San Joaquin basin, California, based on molluscan genera with present day subtropical and tropical distribution. (Addicott, in press)

by Woldstedt's (1954) interpretation of the middle European plant record, more recently, as shown here in Fig. 6. Axelrod and Bailey (1969, Fig. 13) have concurred with this nonfluctuating climatic regime on the basis of a reinterpretation of the Tertiary plant record in western North America.

In support of the concept of a fluctuating, rather than a steadily declining climatic curve for the Tertiary of western United States has been recent evidence from the record of marine invertebrates. On the basis of planktonic foraminifera Bandy (1960) has drawn a climatic curve, shown here in Fig. 7, indicating a series of fluctuations during the earlier Tertiary, with three major high temperature peaks separated by low temperature depressions. Addicott (in press) has recently proposed major climatic fluctuations during both the Oligocene and Miocene of western America on the basis of marine molluscs (Fig. 8). For the same general region, on the other hand, Durham (1950), on the basis of several groups of invertebrates, had previously proposed a steadily declining curve during the Oligocene and Miocene with only a minor warmer fluctuation during the Pliocene.

The increasing interest in Tertiary climates is encouraging and should lead to a productive exchange of ideas during the next few years. Especially important should be the enlistment of other disciplines besides paleobotany in the solution of mutual problems in paleoclimatology.

TRIASSIC, JURASSIC, AND EARLY CRETACEOUS CLIMATES

The Plant Record.

As shown in Fig. 2, the Mesozoic type of plant life was essentially restricted to the Triassic, Jurassic, and Early Cretaceous Periods. Throughout this span of over 110 million years the dominant plant groups were the cycadophytes, the conifers, the ferns, and the ginkos, generally in that order of abundance. Very few fossil forms in any of these major groups are morphologically referable to living genera; many of them, however are referable to living families. Paleoclimatic inferences must accordingly be based on the climatic requirements of related groups at the family level. These are naturally regarded as less certain than are inferences based on generic distributions, and obviously very much less than those based on specific distributions. Nevertheless, results obtained from the overall climatic facies of many Mesozoic assemblages have shown not only internal consistencies but also consistencies with other lines of evidence, including the use of observable morphologic features.

Morphological and Distributional Criteria.

The kinds of morphologic characters that have been used in studies of Mesozoic climates include: 1). relative sizes of coniferous tree trunks, fern fronds, and equisetalean stems, larger sizes denoting warmer climates; 2). presence or absence of tree rings: presence indicating seasonal variations, summer versus winter, or dry versus wet; and absence of rings denoting uniform, generally warm climate; relative thickness of rings corresponds to relative lengths of seasons; 3). degree of dissection of ginkgoid leaves, the greater the dissection the cooler the climate; 4). associated coal or lignite seams, indicating warm, humid, swamp conditions; 5). cuticular characteristics: cuticle thick or thin; distribution and character of stomata: for example, stomata sunken, arranged in grooves, and protected by hairs denotes dry climates.

In addition to morphologic features, the following distributional observations have been used in connection with Mesozoic climatic studies:

(1) Widespread versus restricted occurrences of similar floral assemblages: regardless of taxonomic composition, very widespread distribution of generally comparable forests denotes a lack of appreciable latitudinal zonation, for example, the Jurassic spread from the Arctic to the Antarctic.

(2) The relative abundance and diversity of species: greater numbers and more diversity, generally considered the normal gradient from higher latitudes to the equatorial zone, as at the present time.

Systematics.

The remoteness of taxonomic relationships between Mesozoic and modern plant groups makes the application of fossil plants to Mesozoic climatic

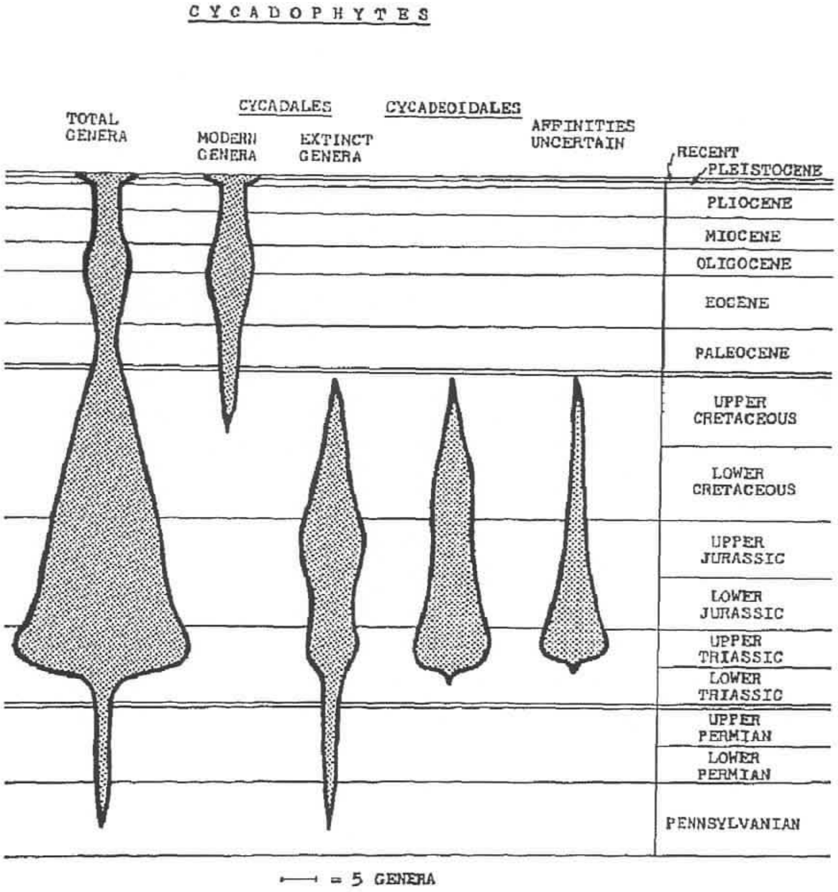

FIG. 9. The geologic record of the genera of cycadophytes.

studies much more difficult than to studies involving post-Mesozoic plant groups. The degree of remoteness is illustrated in Fig. 9, which shows that in the dominant Mesozoic group, the cycadophytes, very few living genera have been recorded as far back as the Jurassic. Obviously, the use of the climatic requirements of living cycad genera for comparative purpose is minimal. The question has been asked as to how reliable the assumption can be that all cycadophytes, extinct and extant, lived under the same subtropical to tropical conditions as the few surviving genera. In the ginkgoalean group, the single living species which thrives under temperate conditions, is the only possible climatic indicator for the many extinct Mesozoic ginkgophytes, whose climatic requirements may have been much broader. The two remaining major groups of the Mesozoic, the ferns and the conifers, are somewhat more useful in paleoclimatic investigations since both groups are still well represented and widely distributed at the present time. Even here, however, relationships of the Mesozoic forms to living taxa are quite remote, so paleoclimatic inferences can only be somewhat generalized.

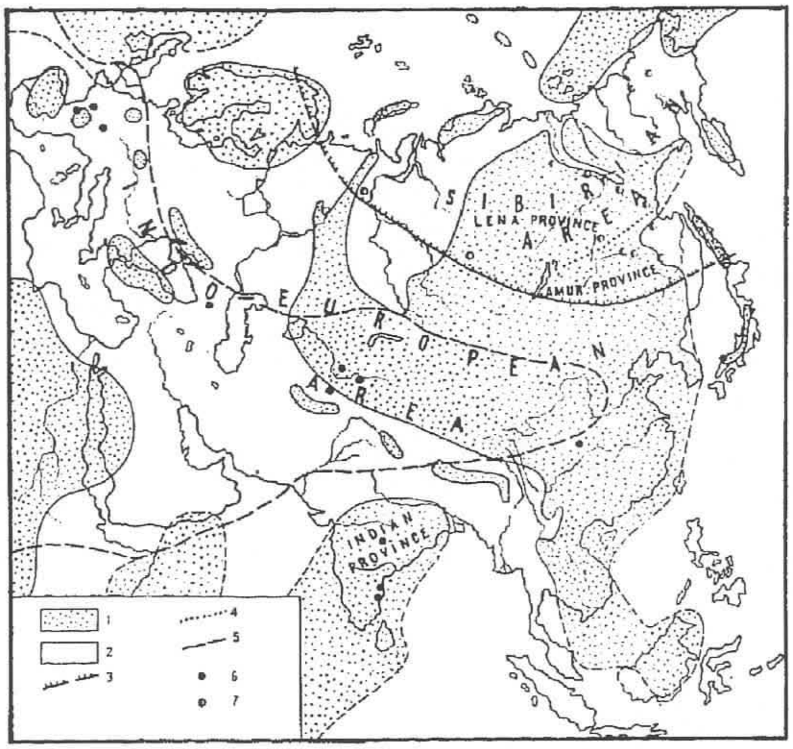

FIG. 10. Paleofloristic areas of the Eurasian region: 1: land; 2: sea; 3: boundary between paleofloristic areas; 4: boundary between paleofloristic provinces; 5: boundary of arid climate zone; 6: main localities of Late Jurassic floras of Indo-European area; 7: main localities of Late Jurassic floras of Siberian area. (Vakhrameev, 1965)

Mesozoic Developments.

Extensive investigations in the USSR, by Vakhrameev (1965) will serve to illustrate both the methods used and the results obtained in the application of typical and wide ranging Jurassic floras to paleoclimatic studies. Vakhrameev recognized over 500 species of Lower, Middle, and Upper Jurassic plants in the USSR. He separated these into two broad "paleofloristic areas," a southern Indo-European area and a northern Siberian area, as shown here in Fig. 10. The Indo-European area is interpreted as having had a humid, tropical climate during most of Jurassic time, because of: 1). abundance of ferns referable to the tropical families Dipteridaceae, Matoniaceae, and Marattiaceae; 2). dominance of both cycads and cycadeoids, presumed to be subtropical to tropical in climatic requirements; 3). presence of only few conifers and ginkgophytes, presumed to be generally temperate; 4). large sizes of the equisetalean remains; 5). recovery of more than twice as many species (over 500) as are found in the floras of the more northerly Siberian area.

Vakhrameev believed the northern Siberian area to have been a more temperate climatic zone on the basis of the following criteria: 1). abundance of temperate types of ferns, and only a few showing relationships to sub-

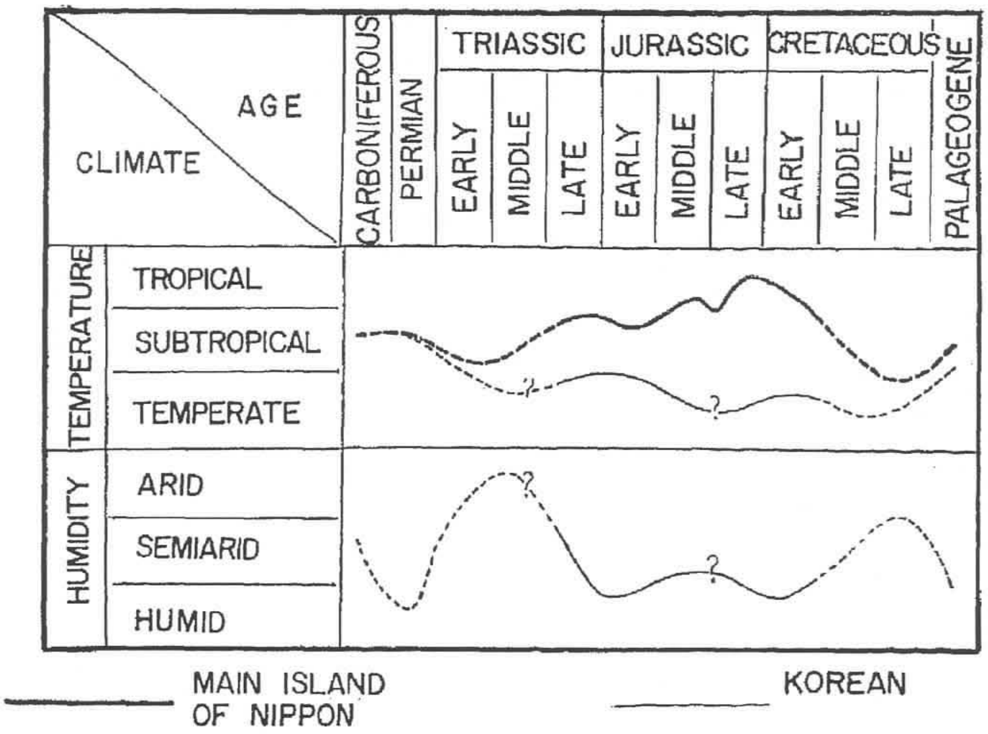

FIG. 11. Paleoclimatic changes during the Mesozoic Era in Nippon and the Korean peninsula. (Kobayashi, 1942)

tropical families; 2). floras made up mainly of conifers and ginkgophytes, presumably a temperate facies; 3). cycads and cycadeoids generally rare; 4). equisetalean remains chiefly of small size; 5). fewer than half as many species present as in the Indo-European area; 6). occurrence of wood with well developed annual tree rings in the Late Jurassic deposits, indicating seasonal changes, presumably from warmer to colder. Vakhrameev further presented evidence that the tropical-temperate boundary shifted its position from time to time, southward in the Middle Jurassic, and a considerable distance northward in the Late Jurassic. In general, his paleoclimatic interpretations agree with those previously proposed by Arkell (1956) on the basis of marine invertebrate faunas.

No comprehensive investigations of North American Jurassic floras and their climatic implications have ever been made. This is a direct reflection of the scarcity of Jurassic plant localities—none in eastern North America, and only a few in the Pacific states and Alaska.

In eastern Asia, on the other hand, Kobayashi (1942) has made paleoclimatic interpretations from a sequence of excellent Mesozoic floras, as shown in Fig. 11. His climatic conclusions were based mainly on five criteria: 1). relationships of the fossil ferns to the tropical families Matoniaceae, Marattiaceae, and Dipteridaceae; 2). similarity of other fossil ferns to the subtropical families Schizaeaceae, Gleicheniaceae, Cyatheaceae, and Polypodiaceae; 3). the southward increase in the number of species belonging to the ferns and the cycadophytes; 4). corresponding northward increases in the number of species of conifers and ginkgophytes; 5). degree of dissection of various types of ginkgoalean leaves, the greater the dissection the cooler the climate.

Turning to Triassic paleoclimatic investigations, Ash (1967) has recently elaborated on the previous work of Daugherty (1941) on the Late Triassic flora of Arizona and New Mexico. Ash has recorded a total of 40 species, belonging to 38 genera, in the flora from the Zuni Mountains. He regards the climate as similar to that of the present warm, humid tropics on the basis of both taxonomic and morphologic evidence. Ferns related to described species, referable to the families Osmundaceae, Dipteridaceae, Matoniaceae, live at the present in the humid tropics. Cycadophyte leaves in the flora appear to be thin, broad, and not reduced, while their stomata are not sunken, are not protected by hairs, are not in deep grooves and have guard cells which either overlap adjacent epidermal cells or are on the same level.

In his work on the flora from and adjacent to the "Petrified Forest" of Arizona, Daugherty (1941, p. 33) had previously concluded that the Late Triassic climate there had been "tropical or subtropical with ample rainfall" as shown by the tropical fern elements, the large size of the logs (up to 120 feet long and 8 feet in diameter), and the wide tree rings present in the petrified trunks. He added, however, that there were evidences of a distinct dry season in view of the high variability of the tree ring layers, wind pollination features in the pollen grains, the presence of bark boring beetles, requiring dry, fallen logs as hosts and charcoal incrustations indicating the prevalence of forest fires.

SUMMARY

In the absence of direct evidence of ancient climates, fossil plants have generally been regarded as among the more reliable criteria for inferring the nature of paleoclimates.

The methods employed in paleoclimatic investigations differ significantly according to the nature of the plant record involved. In the Quaternary, for example, the record is composed almost entirely of plant microfossils—pollen and spores. The recovery and study of these microfossils requires special techniques and instruments which are generally not applicable to the study of pre-Quaternary floras, whose remains are mainly megafossils. It has also been found that the Quaternary microfossils belong almost exclusively to living taxa; at present, however, it is only rarely possible to refer the microfossils to living species, although generic identifications are readily made. The effects of Pleistocene glaciation on vegetation are clearly recognized in the microfossil record. There are still many unresolved problems however, involving both methods and interpretations.

All paleoclimatic inferences based on the plant record depend on the premise that ancient plants lived under essentially the same environmental conditions as they or their most closely related descendants do at the present time. Allowances must be made, however, for the possibility that the present may be a rather unreliable climatic standard for comparisons. It must also be kept in mind that megafossils from successively older floras of the Tertiary Period will be progressively less "closely related" to living taxa and more difficult to identify.

In the study of pre-Quaternary climates, the inherent difficulties have in large part been overcome by the application of two separate and independent methods: firstly, reliance on distinctive morphologic features of various organs, especially leaves and wood, which have climatic implications; and secondly, dependence on the overall climatic facies of the whole assemblage of ancient plants, rather than on a single or a limited number of component taxa.

On the basis of the plant record, Tertiary climates changed from considerably warmer conditions in the earlier portions of the Period to cooler conditions in the later portions. There are at present differences of opinion as to whether the cooling trend was a steady decline or was marked by a few to many fluctuations. Because of their remoteness from modern plants, paleoclimatic inferences based on pre-Late Cretaceous floras have been made mainly on relevant morphological features. Evidence suggests that the Triassic, Jurassic, and Early Cretaceous climates were more uniform and warmer than at present with minor reversals toward cooler or drier conditions.

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